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Modeling in Biology

Assignment 3

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Question 1: A numerical exploration of the Lorenz system

We first consider the three dimensional Lorenz system shown below.

$$\dot{x} = \sigma(y - x)$$

$$\dot{y} = rx - xz - y$$

$$\dot{z} = xy - bz$$

To get a good understanding of the system, we can start by finding the fixed points of the system by setting all of the equations to zero such that $\dot{x} = \dot{y} = \dot{z} = 0$. We obtain that the fixed points are:

$$x* = (0,0,0) \; and \; \left(\pm\sqrt{b(r-1)}, \pm\sqrt{b(r-1)}, r-1\right)$$

From the form of the fixed points, it can be seen that (0,0,0) is always a fixed point, but the other fixed point only appears when $r > 1$. When $r < 1$, the fixed points are imaginary and are not seen on the phase plane.

We can also calculate the Jacobian of the system to obtain the stability analysis of the system. The Jacobian is as follows:

$$Jacobian_{(x,y,z)} = \begin{pmatrix} -\sigma & \sigma & 0 \\ r-z & -1 & -x \\ y & x & -b \end{pmatrix}$$

From this point, we can calculate the eigenvalues of the system via Matlab to determine the stability of all the fixed points. In the table below, we change the value of r and determine the eigenvalues of the jacobian for both the (0,0,0) fixed point and the other two fixed points. In the following analysis we fix the values of σ and b:

$$\sigma = 10, b = 8/3$$

r = 10	Fixed Point	Eigenvalues
	0 0 0	5.4659, -16.4659, -2.6667
	4.8990 4.8990 9.0000	-12.4757, -0.5955 - 6.1742i, -0.5955 + 6.1742i
	-4.8990 -4.8990 9.0000	-12.4757, -0.5955 - 6.1742i, -0.5955 + 6.1742i

For r = 10, we can see that (0,0,0) is a saddle node and the other fixed points are considered attracting spirals since two of the eigenvalues are imaginary. Thus, the two fixed points other than (0,0,0) will be the attractors of the system since it can be seen that the real component of the imaginary eigenvalues are negative. This negative real component signifies that the spirals are inward towards the fixed point.

r = 24.5	Fixed Point	Eigenvalues
	0 0 0	10.7865, -21.7865, -2.6667
	7.9162 7.9162 23.5000	-13.6523, -0.0072 - 9.5814i, -0.0072 + 9.5814i
	-7.9162 -7.9162 23.5000	-13.6523, -0.0072 - 9.5814i, -0.0072 + 9.5814i

For *r* = 24.5, the situation is the same as for *r* = 10 with (0,0,0) being a saddle node and the other fixed points being attracting spirals. Again, the two fixed points other than (0,0,0) will be the attractors of the system.

r = 25	Fixed Point	Eigenvalues
	0 0 0	10.9393, -21.9393, -2.6667
	8 8 24	-13.6825, 0.0079 - 9.6721i, 0.0079 + 9.6721i
	-8 -8 24	-13.6825, 0.0079 - 9.6721i, 0.0079 + 9.6721i

For *r* = 25, we have a slightly different case than for *r* = 10 or 24.5. Here we again see that (0,0,0) is a saddle node, but the other two fixed points have become repelling spirals as the real component of the eigenvalues have become positive meaning that they exponentially grow away from the fixed point. Later when we take a look at the phase plane and the bifurcation, we can see that this value of *r* is greater than the Hopf bifurcation point. Furthermore, since our fixed points have become unstable, there are no longer any long-term attractors of the system after the Hopf bifurcation.

r = 45	Fixed Point	Eigenvalues
	0 0 0	-2.6667, 16.1852, -27.1852
	10.8321, 10.8321, 44.0000	-14.6165, 0.4749 -12.6619i, 0.4749 +12.6619i
	-10.8321, -10.8321, 44.0000	-14.6165, 0.4749 -12.6619i, 0.4749 +12.6619i

r = 220	Fixed Point	Eigenvalues
	0 0 0	-2.6667, 41.6195, -52.6195
	24.1661 24.1661 219.0000	-17.2826, 1.8080 -25.9337i, 1.8080 +25.9337i
	-24.1661 -24.1661 219.0000	-17.2826, 1.8080 -25.9337i, 1.8080 +25.9337i

For *r* = 45 and 220, we have a similar situation for when *r* = 25. Since we see the positive real value in the eigenvalue corresponding to two fixed points which are not (0,0,0), they are no longer stable fixed points. Again, for these values of *r*, there are no long-term attractors of the system.

We can see a definite change of behavior between *r* values of 24.5 and 25. This Hopf bifurcation occurs at the r value:

$$r = r_H = \sigma\left(\frac{\sigma + b + 3}{\sigma - b - 1}\right)$$

For our specific values of b and σ, we find that $r_H = 24.736$. In the phase plane analysis, we can see this change of behavior occurring in figure 1. We can see that for *r* = 10 and 24.5, we get a spiral getting attracted to the fixed points (which are the long-term attractors of the system). For $r > 24.5$, we see that there are no longer any long-term attractors, but the behavior is chaotic and does not seem to follow a patter except that the trajectories seem to remain in a bounded area around unstable fixed points. For $r = 10$ and 24.5, it can be seen that the trajectories depend on the initial conditions and will either go to the positive or negative fixed point (figures 2a and 2b).

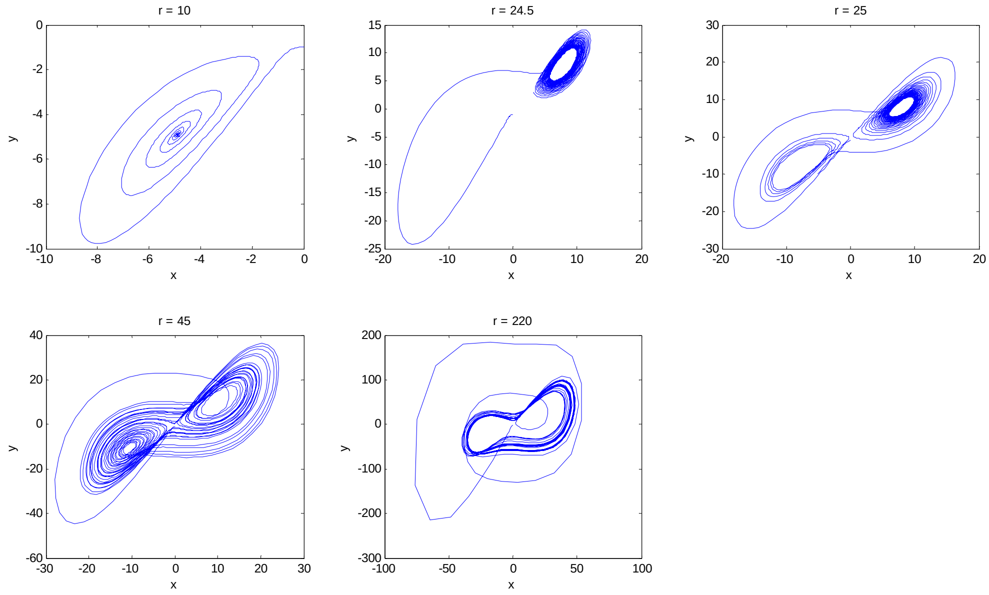
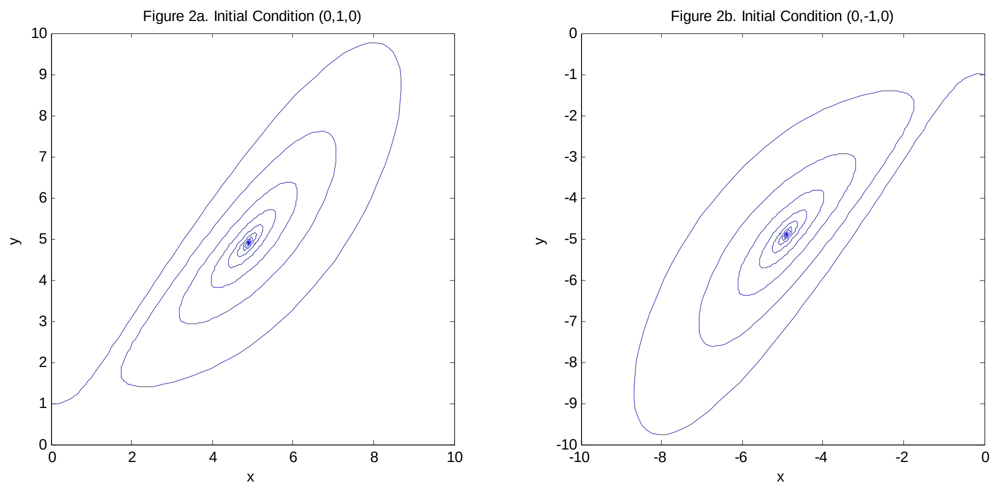


Figure 1. Phase plane *x* vs. *y* for various *r* values



We can further visualize the chaotic nature of the system by plotting the time evolution as shown in figure 3. Chaotic behavior can be seen starting with $r = 25$. From our numerical analysis above, we know that for $r = 24.5$, the system will continue to be periodic and we predict that the long-term behavior will be similar to what is occurring already. For $r > 24.5$, we see a chaotic behavior which is aperiodic but bounded between values, two key elements a chaotic system has.

Another key element a chaotic system has is sensitivity to initial conditions. This is demonstrated by taking two initial values which are very close together.

$$I_1 = (8.8756, 16.1229, 11.5828)$$

$$I_2 = (8.8757, 16.1230, 11.5829)$$

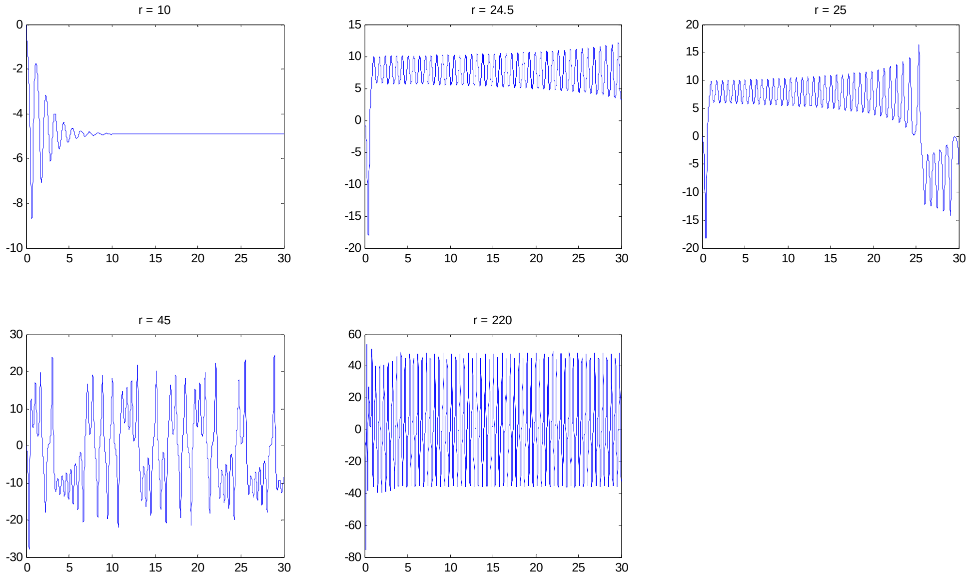
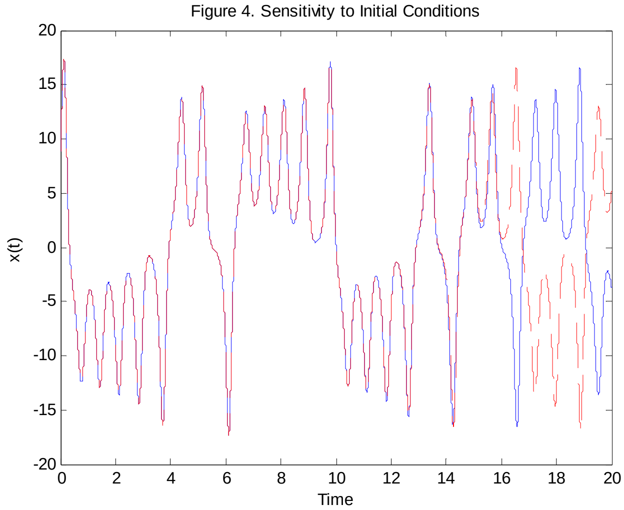


Figure 3. Time evolution of the Lorenz system

The plots of the two initial conditions are shown superimposed in figure 4 (blue corresponding to initial conditions I_1 and red dashed line corresponding to initial conditions I_2).

Figure 4. Sensitivity to Initial Conditions

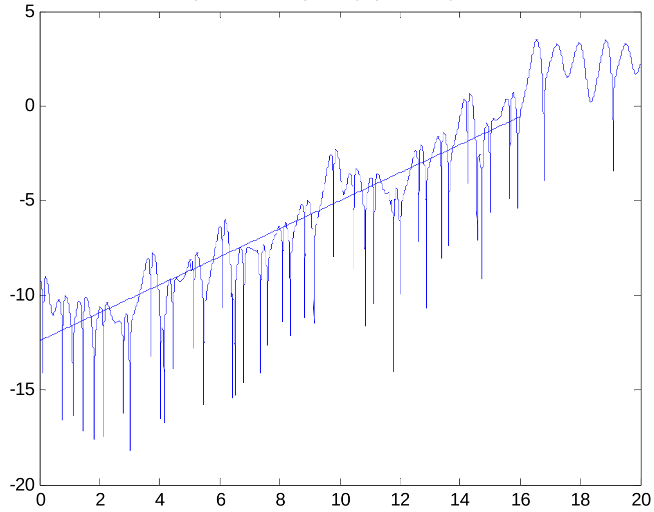


We can see that at approximately when time = 15, the two trajectories begin to diverge significantly. We can calculate the difference to calculate the Lyapunov exponent of the system which is derived from knowing that as time approaches 0, the two trajectories will be very close. As time increases, the two trajectories begin to diverge and the distance between the two is bounded by the elliptical volume in which the trajectories are contained. The Lyapunov exponent, λ, gives the rate of exponential divergence of the two trajectories and gives the limit to which we can predict the behavior of the system. By considering two neighboring trajectories, numerical studies have shown that the following relationship holds true.

$$\|\delta(t)\| \sim \|\delta_0\| e^{\lambda t}$$

Plotting $ln\|\delta_0\|$ vs t (figure 5), we obtain a curve that is close to a straight line with a positive slope λ. A straight line is then fit to the curve to find the value of the slope. The significance of the positive slope is that the trajectories are always diverging. If the slope were to be negative, then the trajectories would be considered converging and the system cannot be considered chaotic. In our system, λ was found to be equal 0.74. The fact that it is positive correlates with the idea that our system is indeed chaotic.

Figure 5. Finding the Lyapunov Exponent



Another interesting aspect of this system is that when the length of integration is increased, the system begins to show chaotic behavior even before the Hopf bifurcation as the plots shown in figure 6 show.

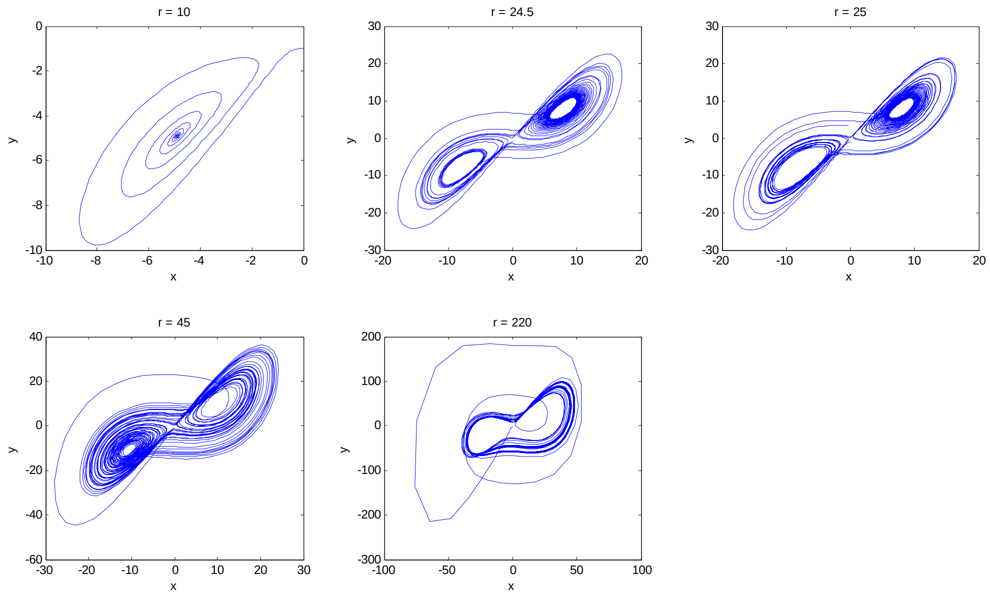


Figure 6. Phase plane x vs. y for t = [0, 50]

It is unclear what the cause is for the strange behavior at extended time period, but we can speculate that this is likely due to the chaotic nature of the function and that the two fixed points are still stable when r is less than r_H.

Question 2: Period doubling and chaos in an oscillatory system

We now consider the system shown below which models some types of neurons exhibiting sub-threshold oscillations.

$$\dot{x} = -y - z$$
$$\dot{y} = x + \frac{1}{5}y$$
$$\dot{z} = \frac{1}{5} + z(x - c)$$

Again, we can find the fixed points of this system using Matlab and calculate their stability. In this system there are only two fixed points shown below.

$$x_1 * = \left(\frac{1}{2}c + \frac{1}{10}\sqrt{25c^2 - 4}, -\frac{5}{2}c - \frac{1}{2}\sqrt{25c^2 - 4}, \frac{5}{2}c + \frac{1}{2}\sqrt{25c^2 - 4}\right)$$
$$x_2 * = \left(\frac{1}{2}c - \frac{1}{10}\sqrt{25c^2 - 4}, -\frac{5}{2}c + \frac{1}{2}\sqrt{25c^2 - 4}, \frac{5}{2}c - \frac{1}{2}\sqrt{25c^2 - 4}\right)$$

From these two fixed points, we can see that a bifurcation occurs at the point where:

$$c = \frac{2}{5}$$

However, the values of c that we are considering are all greater than the bifurcation point. We are only concerned with the following values for c.

$$c = 2.6, 3.5, 4.1, and\ 5$$

In all of these values of c, the two fixed points will appear, so we should consider the stability of each of the points for each value of c. The Jacobian matrix for the system is shown below.

$$Jacobian_{(x,y,z)} = \begin{pmatrix} 0 & -1 & -1 \\ 1 & 1/5 & 0 \\ z & 0 & x - c \end{pmatrix}$$

Calculating the fixed points and corresponding eigenvalues for each value of c, we obtain the following:

For c = 2.6	Fixed points	Eigenvalues
	2.5845, -12.9226, 12.9226	-0.0000 + 3.7309i, -0.0000 - 3.7309i, 0.1846
	0.0155, -0.0774, 0.0774	-2.5580, 0.0868 - 0.9984i, 0.0868 + 0.9984i

Here, we see that for c = 2.6, one fixed point is a center with respect to the *xy* plane (the complex eigenvalues only have an imaginary part) while the second fixed point is unstable, as determined by the positive real part of the eigenvalue.

For c = 3.5	Fixed points	Eigenvalues
	3.4885, -17.4427, 17.4427	-0.0000 + 4.2942i, -0.0000 - 4.2942i, 0.1886
	0.0115, -0.0573, 0.0573	0.0923 - 0.9963i, 0.0923 + 0.9963i, -3.4732

For c = 3.5, the first point is again a center with respect to the *xy* plane while the second fixed point is unstable. However, the second point is an unstable spiral with respect to the *xy* plane and not the *yz* plane as seen when c = 2.6.

For c = 4.1	Fixed points	Eigenvalues
	4.0902, -20.4511, 20.4511	-0.0000 + 4.6313i, -0.0000 - 4.6313i, 0.1902
	0.0098, -0.0489, 0.0489	0.0943 - 0.9957i, 0.0943 + 0.9957i, -4.0789

For c = 4.1, the stability is the same as for when c = 3.5.

For c = 5	Fixed points	Eigenvalues
	4.9920, -24.9599, 24.9599	-0.0000 + 5.0949i, -0.0000 - 5.0949i, 0.1920
	0.0080, -0.0401, 0.0401	-4.9842, 0.0961 + 0.9953i, 0.0961 - 0.9953i

For c = 5, the first fixed point is again a center, but the second fixed point reflects the stability found when c = 2.6 (ie the unstable spiral is now found in the *yz* plane.

Let us take a look at the implications of these fixed points by plotting a phase plane. First we investigate x vs. y in figure 7.

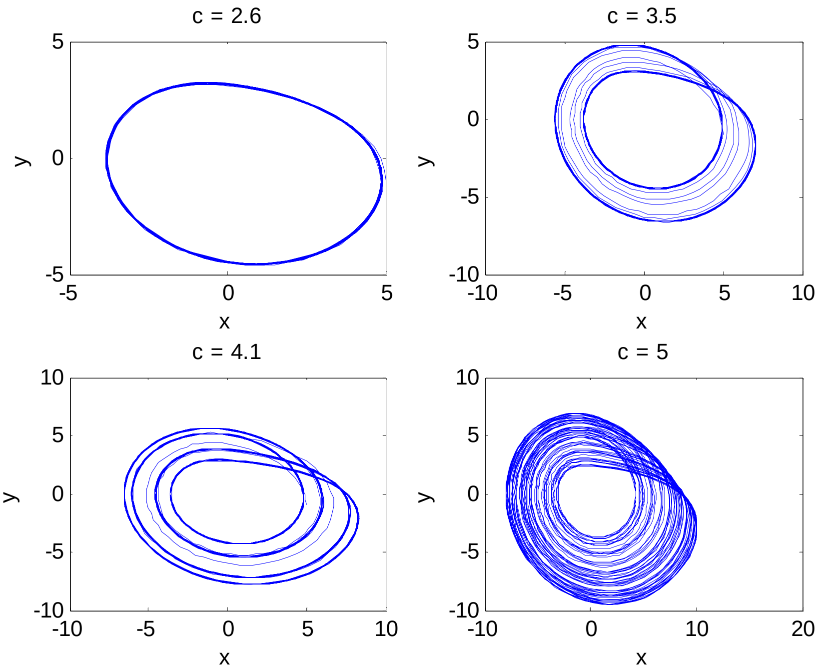


Figure 7. x vs. y phase plane for various c values. Initial conditions [5, -1, 1]

In figure 7, we start with c = 2.6 and see a closed line suggesting a periodic solution because of the limit cycle formed. When c is increased to 3.5, the limit cycle seems to loop twice before closing, suggesting that a bifurcation occurs (a period-doubling bifurcation) between 2.6 and 3.5. When c is further increased to 4.1, the limit cycle loops four times before closing, and when *c* is increased even further to 5, the limit cycle seems to loop several times before closing. Again, another bifurcation occurs between c = 3.5 and 4.1, while it would seem that several more bifurcations occur between c = 4.1 and 5.

The global attractors of the system are the limit cycles, but through our local stability analysis, we were not able to predict the existence of these. Although we see that the trajectories seem to cross, we must remember that the system is actually three dimensional and we are looking at a projection of the trajectories onto the *xy* plane. As we increase the value of *c*, the trajectories begin to go into the third dimension and folds onto itself to maintain that the trajectories do not cross. As *c* increases beyond 5, we see the existence of a strange attractor whose trajectories, when visualized through a Poincare section, resemble a cantor set.

The period doubling that occurs can be easily visualized by plotting *x* over time (figure 8) and seeing the power spectrum (figure 9).

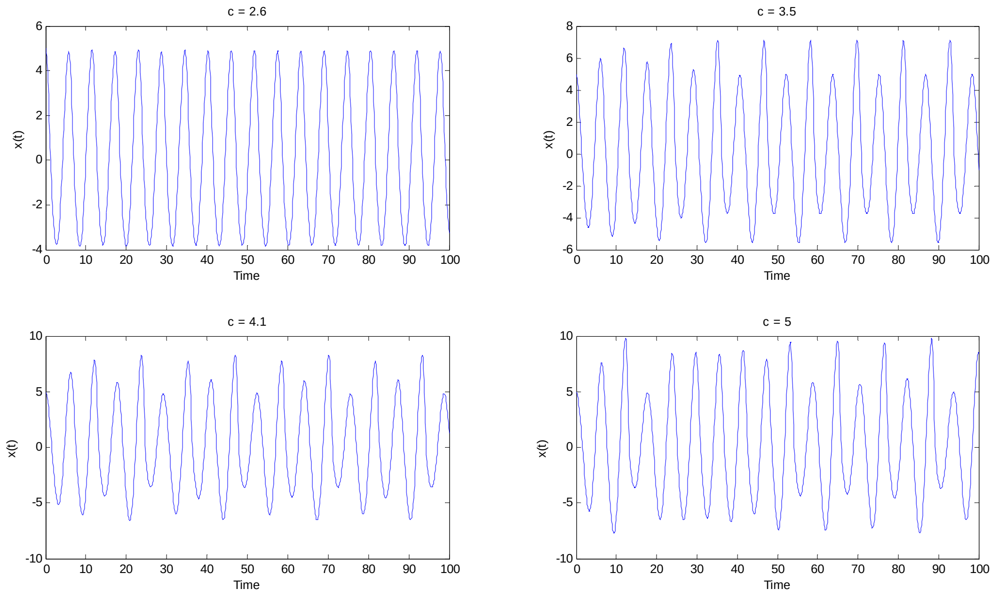


Figure 8. Time evolution of *x* for the Rossler system for various *c* values.

We can see that all of the plots have a periodic behavior but as time increases, it looks like a periodic envelope begins to appear that is half the frequency (or double the period). To verify this phenomenon, we can plot the power spectrum for an extended time to get better sampling (figure 9). We can obtain the power spectrum by using fourier analysis and doing a fourier transform on the signals in figure 8 (except extended in time to produce a greater amplitude in the frequency domain). By doing fourier analysis, we can reduce the signal to its sinusoidal components and plot the frequencies that make up the signal. The major frequencies in the signal will show up as large spikes as seen in figure 9, and we can confirm that we are indeed seeing the period double (or frequency half since there is an inverse relationship between period and frequency).

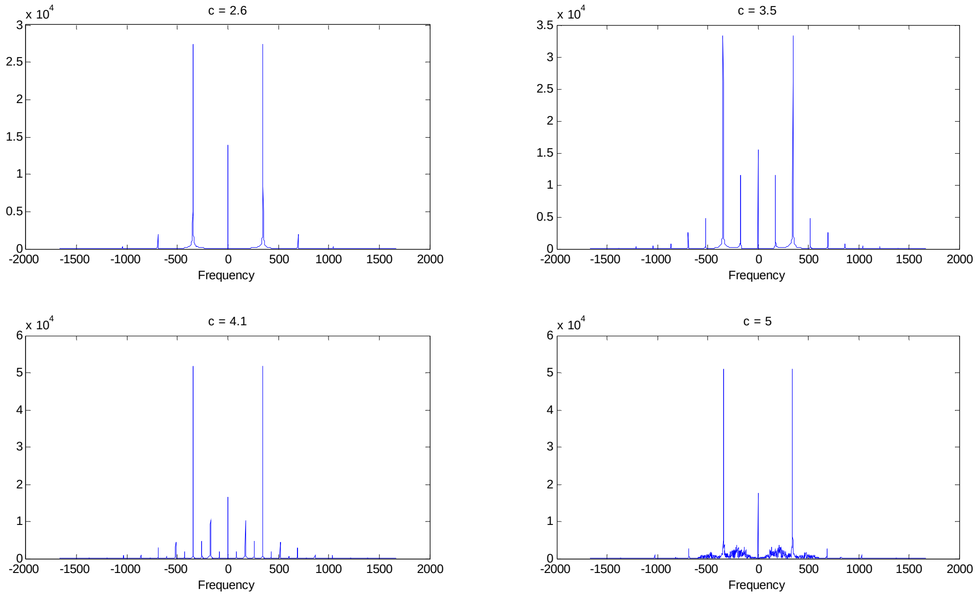


Figure 9. Power spectra of time evolution of *x* for various *c* values.

Indeed, we can see that the major frequency around 300 halves as we increase the value of *c* from 2.6 to 3.5. We again see the frequencies halve increasing to 4.1. However, we don't see the halving very clearly at $c = 5$, suggesting that the period doubles several times to produce the power spectrum seen and individual spikes are no longer visible. In order to see the spikes clearly, it might be possible to extend the time even further, sampling more of the time evolution of *x*.

Question 3: The dynamical response of a spiking neuronal model

In this question we consider the Hodgkin-Huxley equations that were used to model neuronal spiking. The four-dimensional model is shown below.

$$\frac{dV}{dt} = -m_\infty[V](V - 0.5) - 26R(V + 0.95) - g_T T(V - 1.2) - g_H(V + 0.95) + I$$

$$\frac{dR}{dt} = \frac{1}{\tau_R}(-R + R_\infty[V])$$

$$\frac{dT}{dt} = \frac{1}{14}(-T + T_\infty[V])$$

$$\frac{dH}{dt} = \frac{1}{45}(-H + 3T)$$

Where the following relationships also hold:

$$m_\infty[V] = 17.8 + 47.6V + 33.8V^2$$

$$R_\infty[V] = 1.24 + 3.7V + 3.2V^2$$

$$T_\infty[V] = 8(V + 0.725)^2$$

For a regular spiking neuron (RS neuron), the values of the constants are as follows:

For a regular spiking neuron (RS neuron), the values of the constants are as follows:

$$g_T = 0.1, g_H = 5, \tau_R = 4.2$$

The plots in figure 10 below show the time trajectories for different injected currents on the time interval [0, 300].

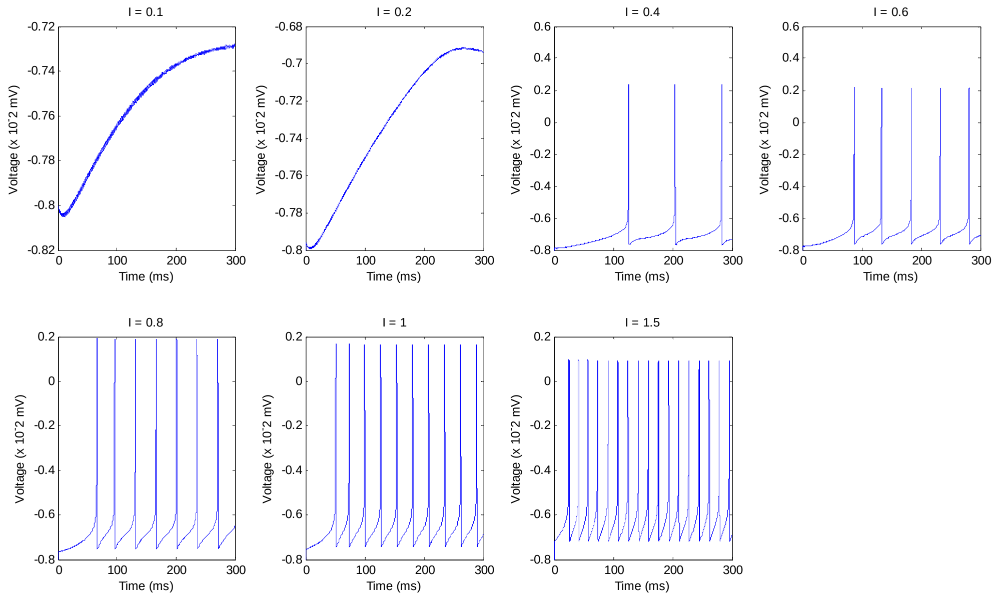
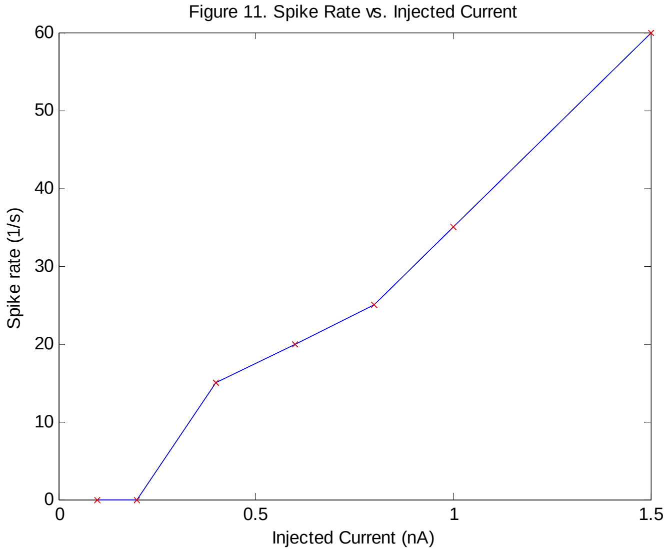


Figure 10. Hodgkin-Huxley model, the time evolution of voltage with varying injected current (I) for regular spiking (RS) cells.

In figure 11, we can see that the spiking rate increases as you increase the injected current. The spiking rate was calculated on the time interval [100 ms, 300 ms] to avoid the irregularity leading up to 100 ms for most of the time trajectories.

Figure 11. Spike Rate vs. Injected Current



From figure 11, we can see that currents below 0.4 V are sub-threshold, but any current 0.4 V and higher do produce spiking behavior in the neuron.

Repeating the calculations for a fast spiking cell where the following parameter values now hold:

$$g_T = 0.25, g_H = 0, \tau_R = 1.5$$

We obtain the plots in figure 13 and 14 for the time trajectories and the spike rate vs. current, respectively.

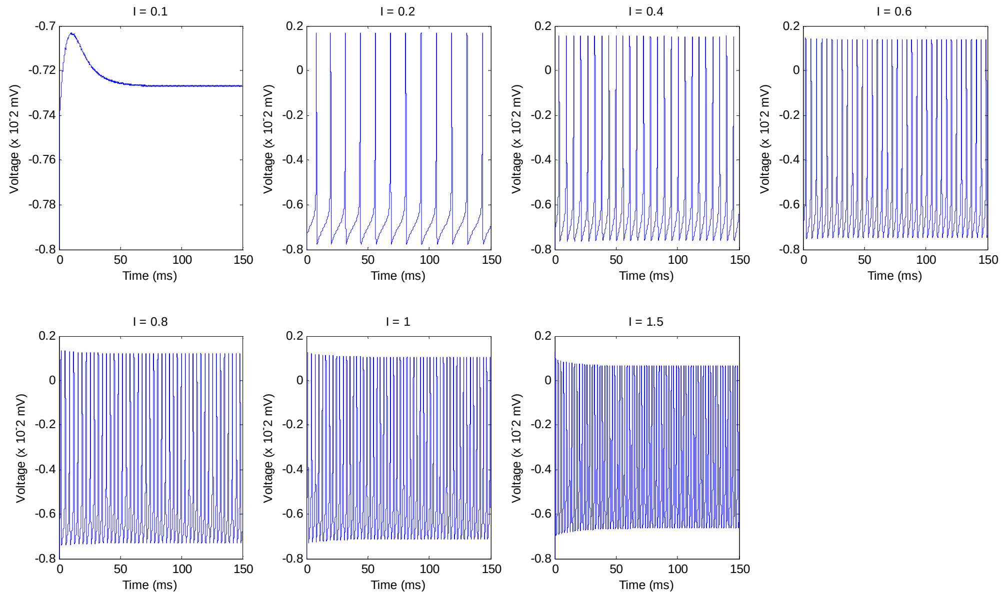
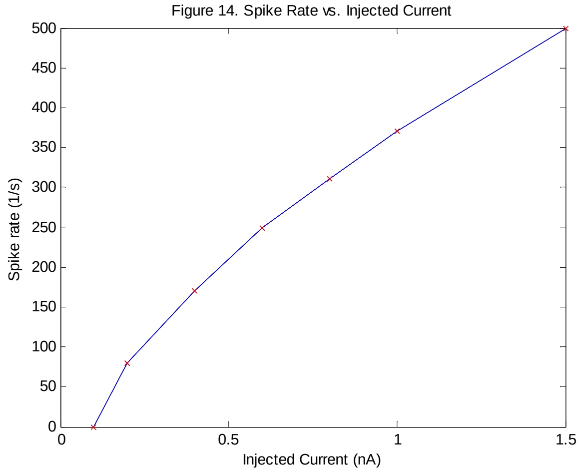


Figure 13. Hodgkin-Huxley model, the time evolution of voltage with varying injected current (I) for fast spiking (FS) cells.

Figure 14. Spike Rate vs. Injected Current



Now we see that only for I = 0.1 is the current sub-threshold. All other currents will induce spiking behavior. Also, we note that the rate of spiking is much higher than the RS cells, reaching a peak of 500 per second as opposed to 60 per second in RS cells (sample interval taken from [50 ms, 150 ms]).

Comparing the RS to FS cells, we can see that the threshold is lower for FS cells, the spiking rate is much faster (by an order of at least 9), but the resting potential and shape of spikes remains the same. The resting potential looks to be about 0.7 $x10^{-2}$ mV.

Another group of neurons is the neocortical neurons that produce 'continuous bursting' under constant current stimulation. The parameters are change again and are shown below.

$$g_T = 2.25, g_H = 9.5, \tau_R = 4.2$$

The time trajectory for an injected current is shown in figure 15.

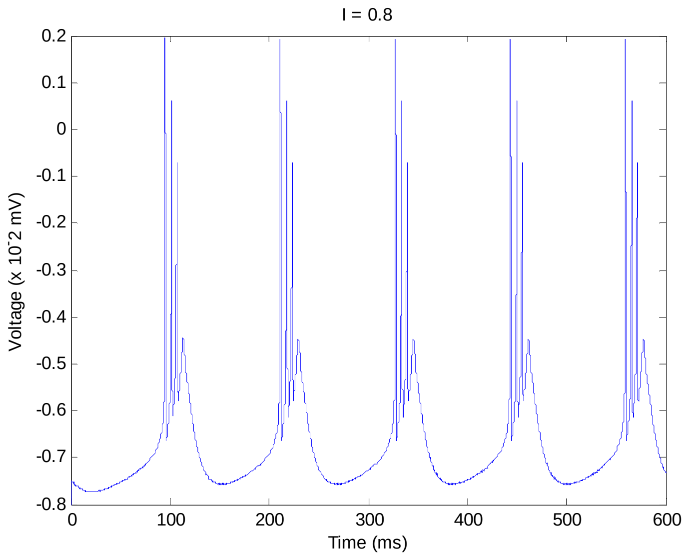


Figure 15. Model for neocortical neurons (CB) producing continuous bursting for a constant injected current of 0.8 nA.

From figure 15, we can easily estimate the inter-burst period. In the interval from 0 to 500, there are 4 spike-regions, so a good estimate for the inter-burst period is 125 ms (or a frequency of 8 per second). We can zoom into one of the bursting periods to get an estimate of the inter-spike period as shown in figure 16.

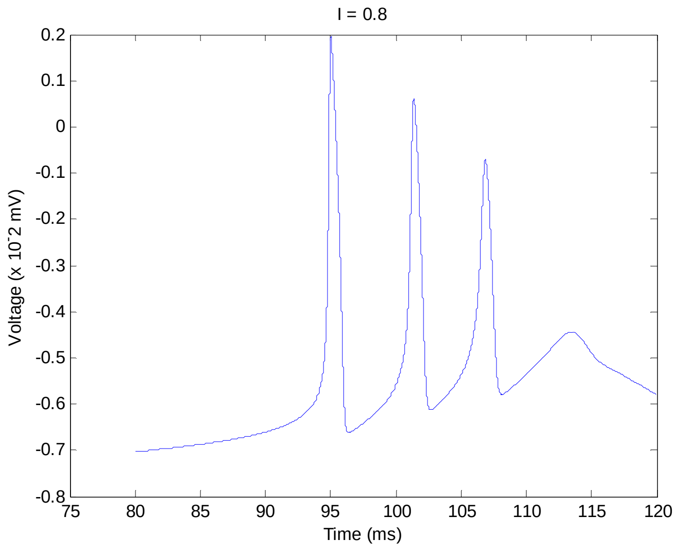


Figure 16. Zoom in of time trajectory for CB cells for injected current of 0.8 nA (see also figure 15)

The inter-spike spacing (or period) is approximately 7 ms corresponding to a frequency of 143 per second. This is significant greater than for RS cells, but much less than for FS cells when comparing to the spike rates for I = 0.8 nA (25 and 300 per second, respectively).